

The braincase of *Anniella pulchra* Gray (Lacertilia: Anniellidae)

by

Olivier RIEPPEL

With 4 figures

ABSTRACT

The braincase of *Anniella* shows no particular similarity to typhlopoid snakes as it would appear from literature studies. The basicranium of *Anniella* shows some convergence to the condition found in snakes. *Anniella* demonstrates the loss of the cavum epiptericum as it had previously been suggested for snakes (RIEPEL 1976).

INTRODUCTION

The head skeleton of the burrowing California limbless lizard, *Anniella pulchra*, has received extensive attention by previous workers already. As early descriptions as that of BAUR (1894) and COE & KUNKEL (1906) include little more than a superficial analysis of the skull. BELLAIRS (1950) and TOERIEN (1950) independently present data on the head anatomy of *Anniella* collected from serially sectioned material. In their analysis of the relationships of the family, McDOWELL & BOGERT (1954) observe many patristic similarities between *Anniella* and the European anguid *Anguis* while similarities between *Anniella* and platynotans are considered to be homoplastic.

The only detailed description of the bony braincase and the soft structures associated with it has been given by TOERIEN (1950). His paper cites a number of characteristics of *Anniella* which prove to be of high theoretical interest. In the course of an investigation of the head anatomy of anguinomorph lizards the occasion was taken to review the structure of the braincase of *Anniella* and to discuss possible implications.

MATERIAL AND METHODS

For the present analysis one specimen of *Anniella pulchra nigra* (MBS. 8331) was dissected. An additional dried skull of *Anniella p. pulchra* was provided through the courtesy of Dr. R. G. Zweifel, The American Museum of Natural History, New York

(AMNH. 95510). Mrs. D. Keller, Zoologisches Institut der Universitaet Basel, with great skill prepared serial sections of a third specimen (*Anniella p. pulchra*, MBS. 12970). The sections were cut 15 thick and stained after BODIAN. They were analysed by simple inspection without any reconstructions made.

IMPLICATIONS FROM PREVIOUS DESCRIPTIONS

TOERIEN (1950) cites a number of features of the braincase structure of *Anniella* which, on the basis of information accumulated since, seem of great theoretical interest and therefore worthy of a critical review.

A major stimulus to reconsider the relationships of squamate reptiles resulted from McDOWELL & BOGERT's (1954) work on anguimorph lizards. According to these authors, the snakes are of platynotan (aigialosaurian) origin. The Typhlopidae they think are wrongly classified with snakes since they are believed to be of a separate dipluglossid (anguinid) origin. *Anniella* on the other hand has its closest relative among the anguines and is therefore grouped by McDOWELL & BOGERT (1954) within their dipluglossid lineage.

Some features of the braincase of *Anniella* as described by TOERIEN (1950) seem to link this genus to *Typhlops* following a re-examination of the latter's head anatomy (RIEPEL, in press), seemingly supporting McDOWELL & BOGERT's (1954) conclusion.

According to TOERIEN (1950), *Anniella* retains a posterior cerebral vein. This vein, leaving the skull through the jugular foramen, is known to persist in *Sphenodon* only among extant lepidosaurs (O'DONOHUE 1920). In squamates, the vein becomes replaced by the occipital vein leaving the skull through the foramen magnum (van GELDEREN 1924). Only in *Amphisbaena* (VERSLUYS 1899) and in *Typhlops* (RIEPEL, in press) a possible homologue of the posterior cerebral vein is known to persist, leaving the skull in association with the vagus nerve: in both cases the homology still needs confirmation through embryological studies. *Anniella* would represent a third case of possible retention of the posterior cerebral vein among squamates.

Following TOERIEN (1950), the posterior part of the Vidian canal of *Anniella* runs in the basisphenoid-prootic suture as it is known to be the case in amphisbaenids (KRITZINGER 1946) as well as in typhlop snakes (RIEPEL, in press) among extant lepidosaurs. The palatine ramus of the facial nerve is said to pass through the prootic bone directly into the Vidian canal.

THE BRAINCASE OF *ANNIELLA PULCHRA*

The bony structure of the braincase of *Anniella* is shown in Fig. 1. There is complete fusion of the basioccipital, basisphenoid, opisthotic and exoccipital bones. The supraoccipital and the prootic remain separate at least in the skull roof.

The crista sellaris is pierced by the abducens nerve as it is typical for lepidosaurs. The dorsum sellae is low, a feature possibly related to the absence of a retractor bulbi muscle (BELLAIRS 1950) which in other lizards takes its origin from the retractor pit in a higher dorsum sellae (SÄVE-SÖDERBERGH 1946).

In *Anniella* the posterior opening of the Vidian canal is seen in a relatively low position below the facial foramen. Both rami of the facial nerve leave the skull through the facial foramen (*contra* TOERIEN 1950). The ramus hyomandibularis runs postero-dorsally across the shaft of the stapes, there giving off the chorda tympani which descends

in front of the stapes. The ramus palatinum enters the Vidian canal together with the cerebral carotid. In the sections the Vidian canal is seen to run between two partially distinct layers of bone representing the fused basisphenoid and parasphenoid. In contrast to TOERIEN's (1950) description it thus runs in a typically lacertilian position. The Vidian canal then opens on the dorsal surface of the basisphenoid within the sella turcica (Fig. 1b). The cerebral carotid may (MBS. 8331) or may not (MBS. 12970) enter the sella turcica through a separate foramen. Within the now dorsally open Vidian canal continues the palatine nerve accompanied by the palatine artery. The above mentioned discernible layers of bone show the nerve and the artery to run along the inner margin

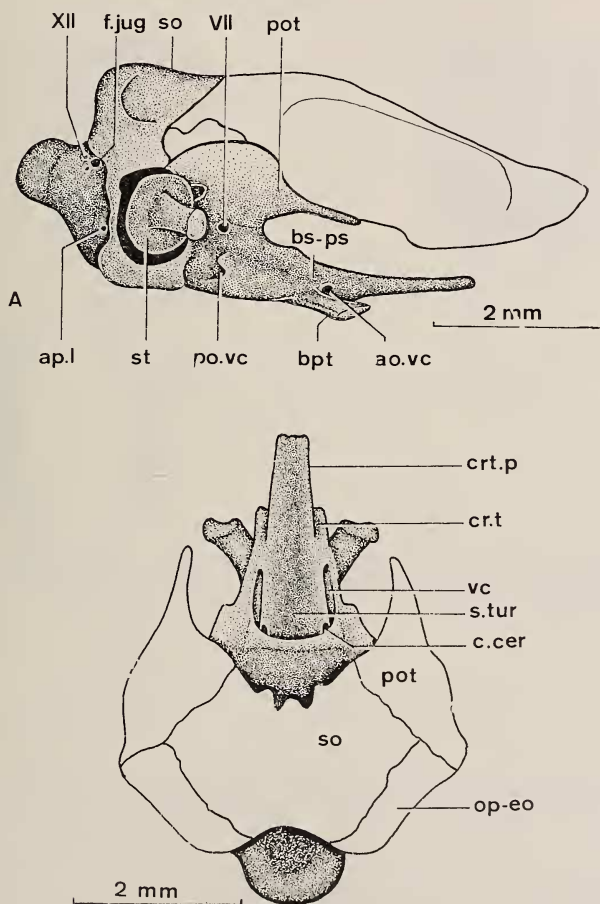
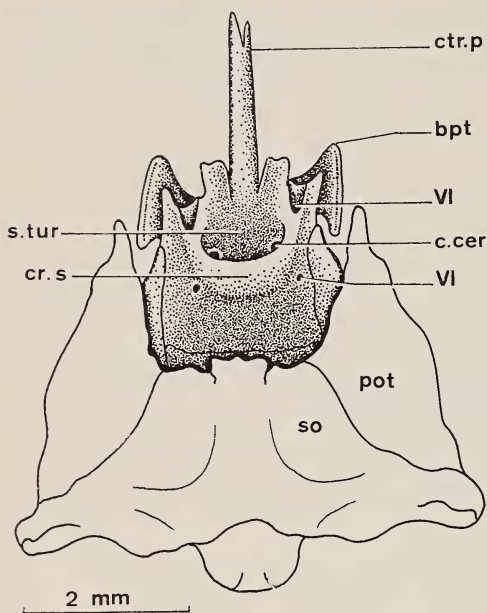


FIG. 1.

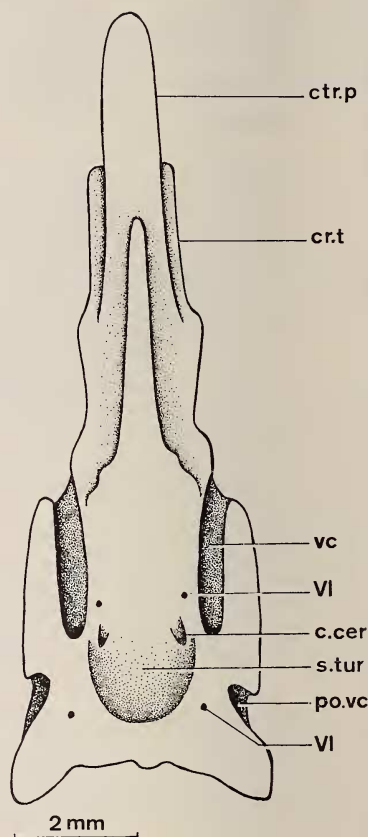
The braincase of *Anniella pulchra nigra* (MBS.8331) A, right lateral view, B, dorsal view. Abbreviations: ao.vc: anterior opening of the Vidian canal; ap. l: apertura lateralis recessus scalae tympani; bs-ps: basisphenoid-parasphenoid complex; bpt: basipterygoid process; c.cer: carotis cerebralis; crt: crista trabecularis; crt.p: cultriform process; f. jug: foramen jugularis; op-eo: opisthotic-exoccipital; pot: prootic; po.vc: posterior opening of Vidian canal; so: supraoccipital; st: stapes; s.tur: sella turcica; vc: Vidian canal; VII: foramen pro n. facialis; XII: foramina pro n. hypoglossus.

of the embryonic fenestra basicranialis (DeBeer 1937). The margins of the basicranial fenestra formed by the basal plate ossify as basisphenoid, while the basicranial fenestra becomes closed by the underlying parasphenoid. Thus, in the region of the sella turcica, the Vidian canal of *Anniella* runs in the dorsal surface of the parasphenoid but, as a



↑ FIG. 2.

The braincase of *Anguis fragilis* (MBS.16491) in dorsal view. Abbreviations: cr.s.: crista sellaris; VI: foramen pro n. facialis. Others as in Fig. 1.



↑ FIG. 3.

The basisphenoid-parasphenoid complex of *Cylindrophis rufus* (MSB.7932) in dorsal view. Abbreviations as in Fig. 1 and 2.

consequence of the extent of the basicranial fenestra, it is not covered by the basisphenoid ossification and therefore remains open dorsally. Further anteriorly, the Vidian canal reenters the bony basicranium to pierce the base of the basiptyergoid process. Thus *Anniella* shows a typical lacertilian course of the Vidian canal differing from other lizards in its dorsal exposure within the sella turcica only. In comparison to *Anguis* (Fig. 2) this appears to result from a lengthening of the bony basal plate corresponding to general proportional changes of the skull (Bellaïrs 1950).

Similar proportional changes may be held responsible for the position of the primary anterior opening of the Vidian canal in primitive snakes (Fig. 3) on the dorsal surface

of the basisphenoid (RIEPEL, ms). But in this case the Vidian canal does not reenter the basisphenoid-parasphenoid complex again, implying different morphogenetic relationships of the expanded bony basicranium.

Within the periotic region the recessus scalae tympani exhibits a specialised condition in that its apertura lateralis forming the occipital recess in other lizards is greatly reduced in *Anniella* (Fig. 1a). The n. glossopharyngeus leaving the skull through the apertura lateralis as in other lizards enters the recessus scalae tympani through a foramen glossopharyngei internum lying just above the apertura medialis recessus scalae tympani (Fig. 4), another specialised feature of *Anniella*. Snakes, too, usually show the presence

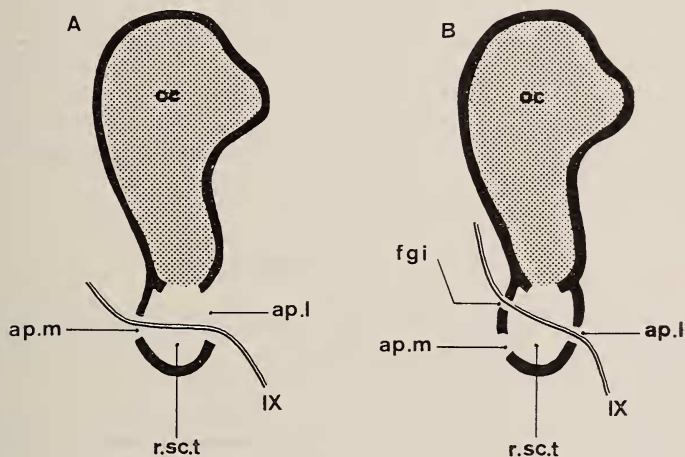


FIG. 4.

Schematic view of the recessus scalae tympani of A. a typical lizard, B. *Anniella*.

Abbreviations: ap.m: apertura medialis recessus scalae tympani; fgi: foramen glossopharyngei internum; r.sc.t: recessus scalae tympani; IX: glossopharyngeal nerve. Others as in Fig. 1.

of a foramen glossopharyngei internum, but there it leads into the cavum vestibuli. The glossopharyngeal nerve then enters the recessus scalae tympani together with the perilymphatic duct through the perilymphatic foramen.

In *Anniella*, the internal carotid passes typically below the stapes after having given off dorsally the stapedia artery. The latter passes above the stapedia shaft, there subdividing into the facial and the mandibular artery. A small vessel originating from the stapedia artery pierces the stapedia shaft as described by TOERIEN (1950). The mandibular artery passes downwards in front of the stapedia shaft to follow the mandibular division of the trigeminal nerve into the lower jaw. *Anniella* thus shows the typical lacertilian condition differing from snakes including *Typhlops* (RIEPEL, in press). The stapedia artery of lizards is considered to be homologous to the facial carotid of snakes. The stapedia artery crosses the stapes in all non-gekkonid lizards: it gives off the mandibular artery above the stapes. The facial carotid does not cross the stapes in snakes: it gives off the mandibular artery in front of the stapes. This seems a phylogenetically more primitive condition, known also from *Spehodon* as well as from gekkonids and pygopodids among extant lizards (GREER 1976).

The vena cerebialis posterior does not persist in *Anniella*, neither passing through the jugular foramen, nor passing through the recessus scalae tympani as described by TOERIEN (1950). Instead there is the typical squamate pattern of a caudally bifurcating vena cerebialis longitudinalis giving rise to the occipital veins (van GELDEREN 1924) leaving the skull through the foramen magnum and fusing laterally into the lateral head vein. The latter crosses the stapes to expand into a large periotic sinus covering the anterior half of the stapedia foot-plate. Anteroventrally, the pterygoid vein originates from this sinus while anterodorsally the lateral head vein reemerges from it. The latter passes ventral to the trigeminal nerves, connected with the prootic sinus through the vena cerebialis media secundaria (BRUNER 1907; van GELDEREN 1924). Anteriorly the lateral head vein passes lateral to the epipterygoid, e.g. lateral to the cavum epiptericum in a snake like fashion (RIEPEL 1976). In all other lizards so far investigated as well as in amphisbaenids (ZANGERL 1944, and personal observation) the lateral head vein passes through the cavum epiptericum. Still, the abducens nerve and the ophthalmic division of the trigeminal nerve pass through the cavum epiptericum in *Anniella*. The peculiar course of the lateral head vein may be the result of a reduction of size of the cavum epiptericum due to extensive parietal downgrowths in *Anniella* and a corresponding reduction of the epipterygoid bone (BELLAIRS 1950; TOERIEN 1950).

RESULTS AND DISCUSSION

As has already been shown the structure of the braincase and associated soft parts does not support any segregation of typhlopoid snakes neither from leptotyphlopoids nor from the basic ophidian pattern (RIEPEL, in press).

A reinvestigation of the cranial structure of *Anniella pulchra* also removes any particular similarities of this genus of diploglossid (*sensu* McDOWELL & BOGERT 1954) affinities to typhlopoid snakes as would appear from the literature (TOERIEN 1950).

The basicranium of *Anniella* shows some similarity to the primitive ophidian pattern but this is easily explained as a result of convergence.

Surprising is the course of the vena capitis lateralis as observed in *Anniella*. The vein runs lateral to the cavum epiptericum in striking contrast to other lizards and to amphisbaenids. In amphisbaenids, parietal downgrowths incorporate the cavum epiptericum into the braincase so that the lateral head vein passes intracranially through the orbito-temporal region.

BELLAIRS & UNDERWOOD (1951) thought the cavum epiptericum to lie in an intracranial position in snakes, too, again due to extensive downgrowths of the parietal closing the braincase laterally. But as the lateral head vein runs extracranially in snakes, I considered the snakes to have lost the cavum epiptericum (RIEPEL 1976). The condition observed in *Anniella* seems to support such conclusion, furnishing an intermediate morphological stage developed in convergence. Parietal downgrowths cause a severe reduction of the epipterygoid bone. This bone, discovered by BAUR (1894), was originally thought to be lacking in *Anniella* by COPE (1892). The space of the cavum epiptericum between the epipterygoid and the dura becomes narrowed and restricted down to the ventrolateral edge of the skull. The vena capitis lateralis assumes a new course lateral to the epipterygoid bone. In snakes, the parietal downgrowths are further expanded now descending down onto the basisphenoid-parasphenoid complex. The epipterygoid bone is lost. The ophthalmic division of the trigeminal nerve together with the abducens nerve assume an intracranial course to emerge from the optic foramen, while the vena capitis lateralis runs extracranially.

ZUSAMMENFASSUNG

Der Hirnschädel von *Anniella* zeigt keine besonderen Ähnlichkeiten zu den Typhlopiden wie es auf Grund von bestehender Literatur zu erwarten wäre. Das Basicranium von *Anniella* zeigt Konvergenzen zu den Schlangen. Ueberdies zeigt *Anniella* die starke Einengung des Cavum epiptericum durch die Entwicklung stark herabsteigender Parietalflanschen. Die laterale Kopfvene verläuft nunmehr lateral des stark reduzierten Epipterygoides. Ein ähnlicher, konvergent verlaufender Entwicklungsgang könnte den vollständigen Verlust des Cavum epiptericum bei Schlangen erklären (RIEPEL 1976).

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Author's address:

Olivier Rieppel
Naturhistorisches Museum, Zoologische Abteilung
Augustinergasse 2,
CH-4051 Basel
